

A new species of tufted-tailed rat, genus *Eliurus* (Muridae: Nesomyinae), from western Madagascar, with notes on the distribution of *E. myoxinus*

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Abstract.—A new species of *Eliurus*, *E. antsingy* (Muridae: Nesomyinae), is described from western Madagascar, only the second one of the genus so far known from this vast and biologically underexplored region of the island. The distribution of *E. myoxinus*, the other species known from western Madagascar, is also amplified on the basis of new collections that have been made over the past decade as interest in small mammals of this region is rekindling.

Résumé.—Une nouvelle espèce d'*Eliurus*, *E. antsingy* (Muridae: Nesomyinae), est décrite pour la région Ouest de Madagascar. Ce n'est que la deuxième espèce du genre connu pour cette vaste région encore biologiquement sous-explorée de Madagascar. La distribution de *E. myoxinus*, l'autre espèce connue pour l'ouest de Madagascar, est aussi étendue grâce aux nouvelles collectes qui ont été faites au cours de la dernière décennie car l'intérêt porté aux petits mammifères est rallumé.

Among Madagascar's nine endemic rodent genera, *Eliurus*, the so-called tufted-tailed rats, is the most speciose with nine currently recognized species (Carleton 1994, Carleton & Goodman 1998). Eight of these nine species inhabit portions of the great humid forest biome (sensu Humbert 1955) of eastern Madagascar, occurring within both lowland and montane rainforest associations (for example, Carleton 1994, Goodman & Carleton 1996, 1998; Goodman et al. 1999). Only one, *E. myoxinus*, the type species of the genus, is known to occupy Madagascar's dryer western and southern landscapes, such as dry deciduous forest and xerophilous scrub formations (Carleton 1994, Goodman et al. 1999). Although some of the disparity in species richness between east and west probably reflects actually lower biodiversity, some may

be plausibly attributed to the historical insufficiency of biological survey of small mammals in Madagascar's drier environments (see Carleton & Schmidt 1990). For example, recent research and collecting in western forests have uncovered four new species of *Microcebus* or mouse-lemurs and resurrected two others from synonymy (Zimmerman et al. 1998, Rasoloarison et al. 2000). This revision and discovery bring to seven the number of *Microcebus* species now recognized from a region that was only a few years ago thought to hold one.

In this paper, we describe a second species of *Eliurus* from western Madagascar. In addition, we report new localities that significantly amplify the known geographic distribution of *E. myoxinus* and provide western records of two forms apparently related to eastern species.

Materials and Methods

Specimens examined consist principally of study skins with associated skulls from the following collections, their museum acronyms as adopted throughout the report contained in parentheses: The Natural History Museum (BMNH, formerly British Museum of Natural History), London; Field Museum of Natural History (FMNH), Chicago; Muséum National d'Histoire Naturelle (MNHN), Paris; Département de Biologie Animale, Université d'Antananarivo (UA), Antananarivo; National Museum of Natural History (USNM, formerly U.S. National Museum), Smithsonian Institution, Washington, D.C. Coordinates used to compose range maps are those given by collectors for recent collections (see Appendix 1) or those estimated by Carleton & Schmidt (1990) for older ones.

A maximum of 7 external and 18 craniodental variables was recorded in millimeters (mm) for each specimen examined. The external variables, most as given by the collector, include: total length of body and tail (TOTL); head and body length (HBL); length of tail vertebrae (TL); hindfoot length (HFL, usually without claw for recent collections); dry hindfoot length (DHFL, with claw as measured by Carleton); ear length (EL); and weight in grams (WT). The 16 cranial and two dental variables (all measured by Carleton) are: breadth of the braincase (BBC); breadth across both incisive foramina (BIF); breadth of the bony palate across the first upper molars (BM1s); breadth across the occipital condyles (BOC); breadth of the rostrum (BR); breadth of the zygomatic plate (BZP); depth of the auditory bullae (DAB); interorbital breadth (IOB); length of bony palate (LBP); length of diastema (LD); length of incisive foramen (LIF); coronal length of maxillary toothrow (LM1-3); length of rostrum (LR); occipitonasal length (ONL); posterior breadth of the bony palate (PPB); postpalatal length (PPL); width of the first upper molar (WM1); zygomatic

breadth (ZB). These were recorded to the nearest 0.1 mm, using handheld calipers accurate to 0.03 mm and following the anatomical landmarks defined and illustrated in Carleton (1994). Morphological terms for the muroid skull generally follow Hershkovitz (1962), Carleton (1980), and Voss (1988).

Due to the small sample sizes encountered for most western samples of *Eliurus*, specimens from localities over a general region were grouped as operational taxonomic units (OTUs), as defined below. To better gauge the significance of interlocality variation among *E. myoxinus*, four samples of a broadly distributed eastern species, *E. tanala*, were included from throughout its range. Catalog numbers, full locality data, and museum sources of all specimens analyzed are provided in Appendix 1. We use the following abbreviations for various types of Malagasy protected areas: PN, Parc National; RF, Réserve Forestière; RNI, Réserve Naturelle Intégrale; RS, Réserve Spéciale.

Eliurus myoxinus.—OTU (1), $n = 17$, from 5 mi E Bevilany, Petriky Forest, and Parcel II, PN d'Andohahela. OTU (2), $n = 13$, from PN de Isalo, 35 mi E Toliara, Forêt de Vohibasia, Forêt de Vohimena, and Forêt de Zombitse. OTU (3), $n = 9$, from Forêt d'Analabe, Beroboka, Kirindy Forest, Morondava, and Tsilambana. OTU (4), $n = 12$, from Forêt d'Analavelona. OTU (5), $n = 11$, from RF de l'Ankarafantsika.

Eliurus new species.—OTU (6), $n = 2$, from Bekopaka. OTU (7), $n = 3$, from the RNI de Namoroka.

Eliurus tanala.—OTU (8), $n = 18$, from PN de Ranomafana and vicinity. OTU (9), $n = 14$, from PN d'Andringitra. OTU (10), $n = 17$, from RS d'Analamazaotra and vicinity. OTU (11), $n = 6$, from RS d'Anjanaharibe-Sud.

Standard descriptive statistics (mean, range, standard deviation) and multivariate analyses were calculated based on specimens of adult age classes (young, full, and old) defined on grades of dental wear. Ju-



Fig. 1. Dorsal, ventral, and left lateral views (about 1.75 \times) of adult crania and mandibles of western species of *Eliurus*: left, *E. myoxinus* (BMNH 47.1603; ONL = 36.7 mm) from 5 mi E Bevilany; right, *E. antsingy* (MNHN 1966.220, holotype; ONL = 41.9 mm) from Bekopaka. (In order to illustrate conformation of a complete mandible, that of MNHN 1966.2222 was substituted for the partially broken left mandible of the holotype.)

veniles and subadults, identified by their complete or partial gray coats and newly erupted or little worn third molars, were excluded. Sample statistics for external dimensions were employed in tabular comparisons as a general index of size differences among populations and species, but were not considered in multivariate summaries. Derivation of canonical variates and principal components was computed using only the 18 craniodental measurements, all of which had been first transformed to natural logarithms. Loadings are expressed as Pearson product-moment correlation coefficients of the principal components or canonical variates with logs of the original skull variables. All analytical procedures

were conducted using Systat (version 9.01, 1999).

Eliurus antsingy, new species

Fig. 1, Table 1

Holotype.—Muséum National Histoire Naturelle number 1966.2220, an adult male prepared as skin and skull (original number 86), collected 1 July 1964 by J. M. Klein.

The round skin is roughly prepared but intact, the hind feet unconventionally folded forward under the ventrum. It bears two tags affixed to the right hind foot, the collector's original skin label and a later one identifying the collection of the MNHN, Paris. The skull is mostly intact, with minor

breakage of the posterior hard palate and pterygoid processes; the halves of the lower jaw are separated, and both dentaries are missing the tips of the coronoid and angular processes. The habitat is sparingly noted on original tags as "en forêt."

No external measurements are found on the original labels. Approximate dimensions, inferred by measurement of the dry museum skin, are: total length, 300+ mm; tail length, 140+ mm; and hind foot length, 30+ mm.

Type locality.—Madagascar, Toliara Province, Antsingy Forest, near Bekopaka, about 19°07.5'S, 44°49.0'E.

Original tags read only "Bekopaka, Antsingy." *Tsingy* is a type of geological formation, with a characteristic vegetational community, that commences about 3 km to the east of the village of Bekopaka and is enclosed within a reserve that has been recently reclassified as the Parc National de Bemaraha. Formerly much of the forest in this region was within a protected area, variously called the RNI de l'Antsingy or the RNI de Bemaraha; only the southern half has recently been regazetted as the PN de Bemaraha.

In discussions with M. Dokobe, who collaborated with J. M. Klein during the mission to Bemaraha in July 1964, Goodman learned that the site where the MNHN specimens were collected is located to the east of the former Bekopaka aviation field (pers. comm. in Antsalova, Feb 2001). Dokobe confirmed that the animals were trapped in typical tsingy forest, near the trail connecting Bekopaka and Andriandriambe, and we estimate the coordinates of the type locality to be approximately 19°07.5'S, 44°49.0'E.

Diagnosis.—A species of *Eliurus* characterized by large size (ONL = 40–44 mm), correspondingly robust molars (LM1-3 = 5.5–6.0 mm), relatively long incisive foramina (LIF/LD = 56%), and large auditory bullae. Tail tuft composed of dark hairs to the tip, not bicolored. Alveolus of lower incisor short, not terminating laterally as a capsular process.

Table 1.—Comparison of selected external and craniodental measurements of specimens of *Eliurus antsingy* from the type locality, Bekopaka, and the Réserve Naturelle Intégrale de Namoroka.

| Variable | Bekopaka | | RNI de Namoroka (n = 3, 4) |
|----------|-------------------|-------------------|-------------------------------|
| | MNHN 1966.2220 | MNHN 1966.2222 | |
| TL | — | — | 161.7 ± 10.2 150.0–169.0 |
| HFL | — | — | 30.6 ± 0.9 29.0–31.0 |
| ONL | 41.9 | 44.1 | 40.5 ± 0.8 39.8–41.4 |
| ZB | 20.8 | 21.8 | 19.1 ± 0.4 18.6–19.4 |
| BBC | 16.3 | 15.8 | 15.3 ± 0.2 15.0–15.5 |
| IOB | 5.9 | 6.1 | 6.0 ± 0.1 5.9–6.1 |
| LR | 14.8 | 15.1 | 13.4 ± 0.6 12.9–14.0 |
| BR | 7.4 | 7.5 | 7.0 ± 0.2 6.7–7.1 |
| PPL | 14.7 | 15.1 | 14.5 ± 0.2 14.3–14.7 |
| LBP | 7.8 | 7.7 | 7.4 ± 0.1 7.3–7.5 |
| LIF | 6.7 | 6.8 | 6.3 ± 0.1 6.2–6.4 |
| BIF | 3.1 | 2.8 | 2.6 ± 0.1 2.5–2.7 |
| LD | 11.7 | 12.4 | 11.2 ± 0.5 10.9–11.8 |
| BM1s | 8.0 | 8.3 | 7.5 ± 0.2 7.3–7.6 |
| PPB | 6.1 | 6.0 | 5.5 ± 0.2 5.3–5.7 |
| DAB | 6.0 | 6.4 | 5.6 ± 0.05 5.5–5.6 |
| BZP | 3.5 | 4.3 | 3.8 ± 0.1 3.7–3.9 |
| BOC | 9.5 | 9.6 | 9.0 ± 0.2 8.8–9.2 |
| LM1-3 | 6.00 | 5.65 | 5.69 ± 0.14 5.51–5.85 |
| WM1 | 1.65 | 1.58 | 1.49 ± 0.03 1.45–1.53 |

Referred specimens.—MNHN 1966.2222, an adult female from Bekopaka, also noted as from Antsingy; collected 1 July 1964 by J. M. Klein and prepared as skin and skull (original number 85). FMNH 167563–167566, all young to fully adult females from the RNI de Namoroka, collect-

ed June 1999 by M. Anselme Toto Volahy and each prepared as skull with whole carcass in fluid. M. Toto Volahy trapped mammals in two different sites within the reserve, both in dry deciduous forest. Unfortunately, the collector's field tags for the specimens listed were lost and it is not possible to associate them with the original data.

Distribution.—Known only from the type locality and the RNI de Namoroka, western Madagascar.

Description.—Fur texture relatively soft and fine. Cover hairs of dorsal pelage bicolored or tricolored: basal three-quarters a medium plumbeous gray and the distal one-quarter pale buff, some hairs faintly tipped with a third band of dusky brown. Cover hairs 9–11 mm in length over middle rump. Guard hairs medium brown, only slightly longer than cover hairs. General effect of upperparts a dark drab brown to brownish-gray. In specimens from Bekopaka, cover hairs of chest, abdomen, and inguinum bicolored, basal half pale gray and distal half cream to bright white; hairs over chin and throat monocolored white in both specimens, a tract of creamy white hairs extending over the midventer of MNHN 1966.2222; general effect of underparts a medium gray. All specimens from Namoroka with entire venter plain white to pale buff, their underparts contrasting sharply with dorsum; one individual (FMNH 167564) with intense buff to pale ochraceous over thorax, grading to buffy white over the abdomen. Tops of forefeet and hindfeet covered with silvery white hairs, concentrating to form a loose tuft at base of claws that extends to or slightly beyond their tip.

Hindfeet comparatively broad, toes appearing short proportional to the length of the tarsus-metatarsus; HFL, as measured on the dry (toes slightly curled) and fluid specimens, about 29–31 mm, shorter than hind foot of *E. tanala*. Plantar pads six and arranged as per genus, but size large, extremely bulbous and packed very close to-

gether; hypothenar pad as big as an interdigital. Pinnae rounded and relatively small (about 20 mm as measured on the fluid preserved specimens), in proportion resembling those of *E. majori*; color dusky brown externally and clothed with fine brown hairs, paler brown internally and sparsely covered with fine white hairs. One pair each of axillary, abdominal, and inguinal mammae present, total = six (as confirmed on MNHN 1966.2222).

Tail tuft or brush well developed, noticeably evident over distal 40–50% of caudal length, hairs over fullest section about 12 mm long. Tuft dark to tip, composed of pale brown to dusky hairs; tuft of holotype with some fine white hairs randomly intermixed, but not forming a contradistinctive wholly white tip as observed in *E. tanala*. Tail of MNHN 1966.2222 and FMNH 167566 apparently naturally broken at midsection, terminating as a whorl of dark brown and some white hairs. Caudal epidermis medium gray all around near the base of the tail, becoming slightly to heavily mottled, dorsally and ventrally, toward the tip. Scutellation finely textured.

Cranium large in size, approximating that of *E. ellermani* or the largest *E. tanala*, with the incisors, zygoma, rostrum and mandible correspondingly stout in appearance. Dorsal profile of skull appreciably arched, sloping gradually toward the rostrum and more steeply toward the occiput, not so flat as in *E. tanala* of similar size. Rostrum moderately long (LR/ONL = 35%), proportions typical for the genus; zygomatic arches bowed laterally over their midsection, not so parallel-sided as in *E. myoxinus*; braincase relatively wide, rounded and smoothly contoured. Incisive foramina bluntly pointed on their anterior and posterior ends, relatively long and broad for the genus, their diastemal expanse (LIF/LD = 56%) in proportion resembling examples of *E. majori* and *E. penicillatus*. Posterior palatine foramina a single pair of small ovate holes, the palatine bones lacking extensive supernumerary foramina or slitlike vacuities.

Posterior edge of bony palate about even with end of third molars, lacking medial spine; anterior rim of mesopterygoid fossa nearly straight to gently curved. Alisphenoid strut present on both sides in all specimens. Subsquamosal fenestra patent but small, exposing little or none of the brain cavity; hamular process of the squamosal short and stout. Auditory bullae absolutely the largest in the genus, relatively as large as those of *E. myoxinus*.

Enamel face of upper and lower incisors pale yellow-orange in color. Alveolus of lower incisor relatively short, terminating at the level of the coronoid process and appreciably below the sigmoid notch; mandible without prominent capsular process. Molar toothrows long (LM1-3 = 5.6–6.0), about the size of *E. tanala*, absolutely and relatively shorter than those of *E. majori* and *E. penicillatus*; upper and lower third molars smaller than second.

Other external, cranial, and dental features as described for the genus (Carleton 1994, Carleton & Goodman 1998).

Comparisons.—A combination of large physical size, long and wide incisive foramina, and relatively inflated auditory bullae easily distinguishes *Eliurus antsingy* from most members of the genus. For most cranial variables measured, only individuals of *E. ellermani* and some examples of *E. tanala* attain the same large dimensions. Crania of those species, however, possess noticeably smaller auditory bullae, shorter and narrower incisive foramina, a more fenestrated hard palate, and a longer rostrum; further, they exhibit a flatter dorsal profile compared to the distinctly arched shape of *E. antsingy*. The pinnae and hind feet of *E. ellermani* and *E. tanala* are also absolutely longer.

Several characteristics of *E. antsingy* recall examples of *E. majori* and *E. penicillatus*. Like those species, its pinnae appear small and rounded for the size of the animal. Further, the alveolar tract of the lower incisor is somewhat short and does not produce a conspicuous lateral bulge where it

terminates within the mandibular ramus; and the incisive foramina are comparatively long and wide, spanning over 50% of the diasternal length. Unlike *E. majori* and *E. penicillatus*, however, the molar rows of *E. antsingy* resemble most other *Eliurus* in their shorter proportional length, lower crown height, and smaller third molars.

Both *E. antsingy* and its western congener *E. myoxinus* possess relatively large ectotympanic bullae (large, that is, for the size variation observed within *Eliurus*), but the former is not simply an enlarged version of the latter (Fig. 1; Tables 1, 3). The cranium of *E. antsingy* lacks the stocky, squarish appearance of *E. myoxinus*, a contrast imparted by its longer rostrum, comparatively narrow interorbital constriction, and more laterally bowed zygoma. The two differ in configuration of the incisive foramina (long, wide in *E. antsingy* versus short, narrow in *E. myoxinus*) and development of the capsular process (absent in *E. antsingy* versus a moderate bulge in *E. myoxinus*). The pelage of *E. antsingy* is more drably colored than the soft, pale browns of *E. myoxinus*, and its tail tuft is neither as well developed in length of individual caudal hairs nor in extent of tail vertebrae covered as compared with *E. myoxinus*.

Visual impressions of differences in skull size and shape are generally borne out in multivariate analysis of the 18 continuous variables recorded for *E. antsingy* and representative samples of *E. myoxinus* and *E. tanala* (Fig. 2, Table 2). The separation of *E. antsingy* from *E. myoxinus* along the first canonical variate principally reflects its larger cranial size (correlations mostly large and positive); on this axis, the five intact specimens of *E. antsingy* do not stand apart from those of *E. tanala*. Between-group variation summarized by the second canonical variate involves fewer influential variables with only moderate correlations—notably, inflation of the auditory bullae (DAB) and expansiveness of the incisive foramina (BIF, LIF), and to a lesser extent certain indices of cranial breadth (BBC,

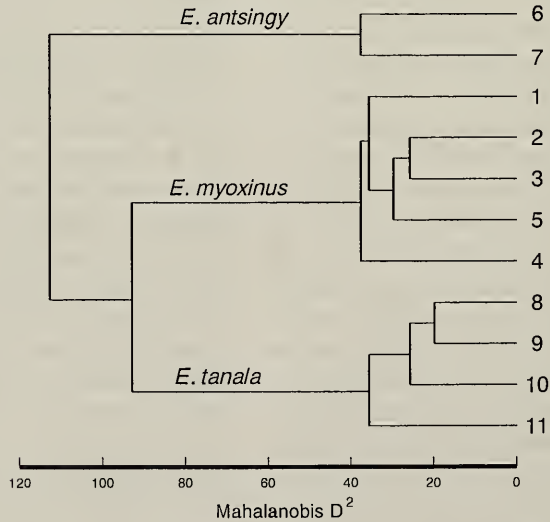
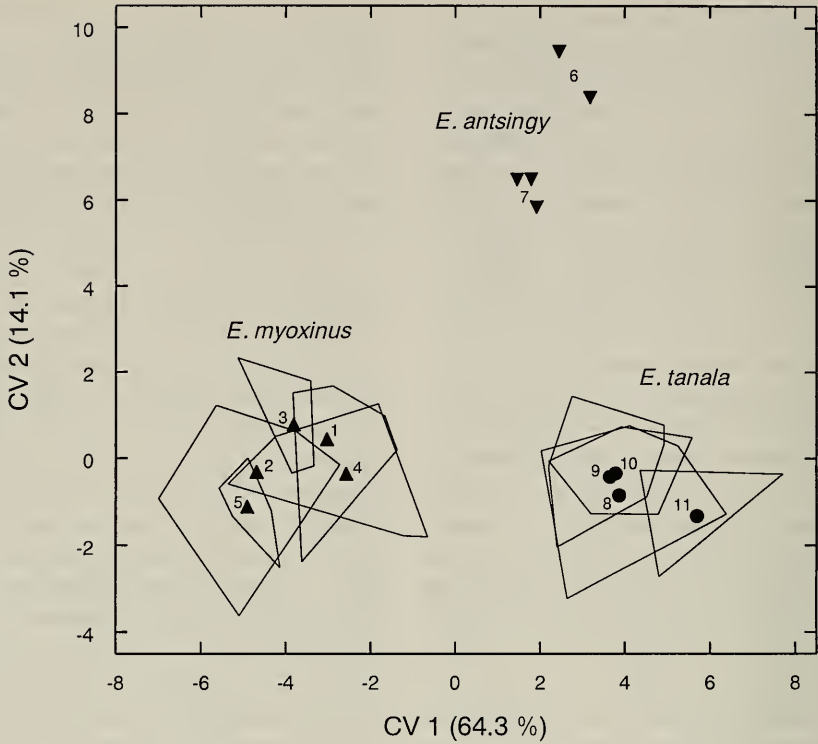


Fig. 2. Results of discriminant function analysis performed on 18 log-transformed craniodental variables, as measured on 122 specimens representing 11 OTUs of *Eliurus* (see Materials and Methods). Top, Projection of individual scores onto the first two canonical variables extracted; polygons for *E. myoxinus* and *E. tanala* enclose the maximal dispersions of specimen scores around a group's centroid, whereas individual scores are themselves plotted for the two samples of *E. antsingy*. Bottom, Phenogram produced from clustering (UPGMA) of Mahalanobis' distances among centroids of the 11 OTUs. See Table 2.

Table 2.—Results of discriminant function analysis of 11 OTUs representing intact specimens of *Eliurus myoxinus* ($n = 50$), *E. antsingy* ($n = 5$), and *E. tanala* ($n = 44$) (see Fig. 2).

| Variable | Correlations | |
|-----------------------|--------------|-------|
| | CV1 | CV2 |
| ONL | 0.93 | 0.17 |
| ZB | 0.80 | 0.19 |
| BBC | 0.49 | 0.28 |
| IOB | 0.71 | 0.18 |
| LR | 0.95 | 0.04 |
| BR | 0.77 | 0.09 |
| PPL | 0.74 | 0.20 |
| LBP | 0.91 | -0.23 |
| LIF | 0.70 | 0.44 |
| BIF | 0.34 | 0.50 |
| LD | 0.93 | -0.04 |
| BM1s | 0.92 | 0.07 |
| PPB | 0.60 | 0.33 |
| DAB | 0.06 | 0.59 |
| BZP | 0.72 | 0.07 |
| BOC | 0.85 | 0.32 |
| LM1-3 | 0.91 | 0.14 |
| WM1 | 0.87 | 0.10 |
| Canonical correlation | 0.97 | 0.89 |
| Eigenvalue | 16.5 | 3.2 |
| % Variance | 64.3 | 14.1 |

BOC, PPB). In each instance, the specimens of *E. antsingy* are exceptional for their relatively greater development, especially as compared with the similarly sized *E. tanala*.

Remarks.—Acquisition of additional specimens of *E. antsingy* is needed to bring taxonomic illumination to the differences remarked between the two examples from Bekopaka, the type locality, and those from the RNI de Namoroka. The latter animals are consistently smaller in size (Table 1), and their ventral pelage is wholly white to pale buff in marked contrast to the gray colored ventrum of the holotype from Bekopaka. The tone of the entirely white venters in the Namoroka series resembles the swath of white observed on the abdomen of MNHN 1966.2222 from Bekopaka, and similar variation in ventral pelage coloration has been noted among populations of *E. tanala* and *E. webbi* (Carleton 1994,

Carleton & Goodman 1998). Moreover, while acknowledging that existing sample sizes of *E. antsingy* are smaller than desirable, the amount of morphometric divergence revealed between the Bekopaka and Namoroka specimens approximates that found among larger geographic samples of widely ranging species, such as *E. myoxinus* and *E. tanala* (Fig. 2). In view of their other similarities in cranial shape and qualitative features of the skull and skin, we provisionally refer the Namoroka specimens to the new species and urge the need for continued study to clarify the interpopulational variation noted.

Little is known about the natural history of *E. antsingy*. The two specimens collected by Klein near Bekopaka were obtained in traps placed on the ground in typical *tsingy* forest habitat (M. Dokobe, pers. comm.).

The sites within the PN de Bemaraha and the RNI de Namoroka are separated by about 300 km (by air). The principal exposed geological formation within the PN de Bemaraha is derived from Mesozoic limestone, and the forest cover across this zone is relatively intact. Thus, we suspect that *E. antsingy* probably occurs throughout much of the Bemaraha complex. To the north of this zone, a break occurs in the Mesozoic limestone formation, which reappears as a series of isolated geological islands all the way north to and including Namoroka (Du Puy & Moat 1998). Within the intermediate zone there are two protected areas—the RS de Maningozy, which rests on sandstone and unconsolidated sands, and the RS de Kasijy, a portion of which occurs on Mesozoic limestone. Further survey work is needed to document whether *E. antsingy* inhabits these intermediate zones.

At the type locality of Bekopaka, Klein collected a third specimen (MNHN 1966.2221) of *Eliurus* together with the two examples of *E. antsingy* described above. The fact that the individual was collected at a later date (13 September 1964) and on a different trip ("Mission no. 7") suggests

that Klein captured it in a different area or microhabitat. The animal is not representative of either *E. myoxinus* or *E. antsingy*. Overall size is large (ONL = 44.3, LM1-3 = 5.85), resembling the dimensions of *E. antsingy* and the most robust samples of *E. tanala* (e.g., those from the northern highlands; Carleton & Goodman 1998). Approximate external dimensions, as measured on the dry skin (no field recorded data) are: total length, ca. 340 mm; tail length, ca. 160 mm; hind foot length, 34+ mm; and ear length, 22+ mm. The upperparts are a pale, grayish-brown; the underparts are entirely creamy white, from the chin to the inguinal region, and contrast sharply with the brown dorsum. The tail tuft is about 70 mm long and consists of two colors arranged in three bands: proximal (ca. 30 mm) and terminal (ca. 10 mm) sections of light brown caudal hairs, separated by a middle segment of purely white hairs (ca. 30 mm). Collection of additional specimens is needed to determine whether this three-banded tuft pattern is typical of the population. A short, terminal dark section is observed, albeit rarely, among samples of *E. tanala*, which otherwise possess a bicolored tuft composed of dark hairs proximally and white hairs towards the tip. The pale brown pinnae seem proportionally the largest in the genus, particularly in comparison to the specimens of *E. antsingy*, but the wrinkled condition of the dried pinnae disallows objective confirmation of our impression.

In addition to generous size and relatively stout construction, the cranium of MNHN 1966.2221 exhibits other traits suggestive of *E. tanala* or *E. ellermani* from eastern Madagascar. The rostrum is comparatively long with short and narrow incisive foramina, sharply pointed on both ends. Small supernumerary foramina occur behind the principal pair of posterior palatal foramina, although these are not coalesced as elongate vacuities as found in many *E. tanala*. The subsquamosal fenestra is occluded, the hamular process thus undefined

except at its posteroventral tip where it abuts the mastoid chamber. The capsular projection of the lower incisor is well developed and terminates just below the ventral rim of the sigmoid notch. Principal component analysis of the same craniodental variables disclosed the same array of specimen clusters as obtained in the canonical variates plot, with MNHN 1966.2221 positioned at the very periphery of the *E. tanala* constellation (not illustrated; % total variance explained on PC I and PC II = 71.0 and 6.7, respectively).

Etymology.—The species name is derived from the Malagasy words *tsingy*, which refers to the spectacular pinnacle-like limestone formation (karst) that occurs to the east of Bekopaka (in the Bemaraha reserve complex) and in the RNI de Namoroka, and *an*, a common prefix which means place of.

Additional Distributional Records of *E. myoxinus* Milne Edwards, 1885

As understood by Carleton in 1994, the geographic range of *E. myoxinus* was confined to southern and southwestern Madagascar, principally along or near the coast from the vicinity of Petriky Forest, extreme southeastern Madagascar, to the Forêt d'Analabe, a place just south of the mouth of the Tsiribihina River. The few localities then known (six) represented dry deciduous forest or xerophilous scrub, and none was recorded above 245 m. Subsequent reports have altered this distributional picture of *E. myoxinus* (e.g., Goodman & Ganzhorn 1994, Goodman & Rasoloarison 1997, Goodman et al. 1999), in particular amplifying its distribution in the southwestern interior between the Mangoky and Onilahy rivers (Fig. 3). These localities, and others listed in Appendix 1, have appreciably broadened the known altitudinal span of the species in the southwest, now documented from near sea level to 1250 m (Forêt d'Analavelona). In addition, they have revealed the greater ecological tolerance of

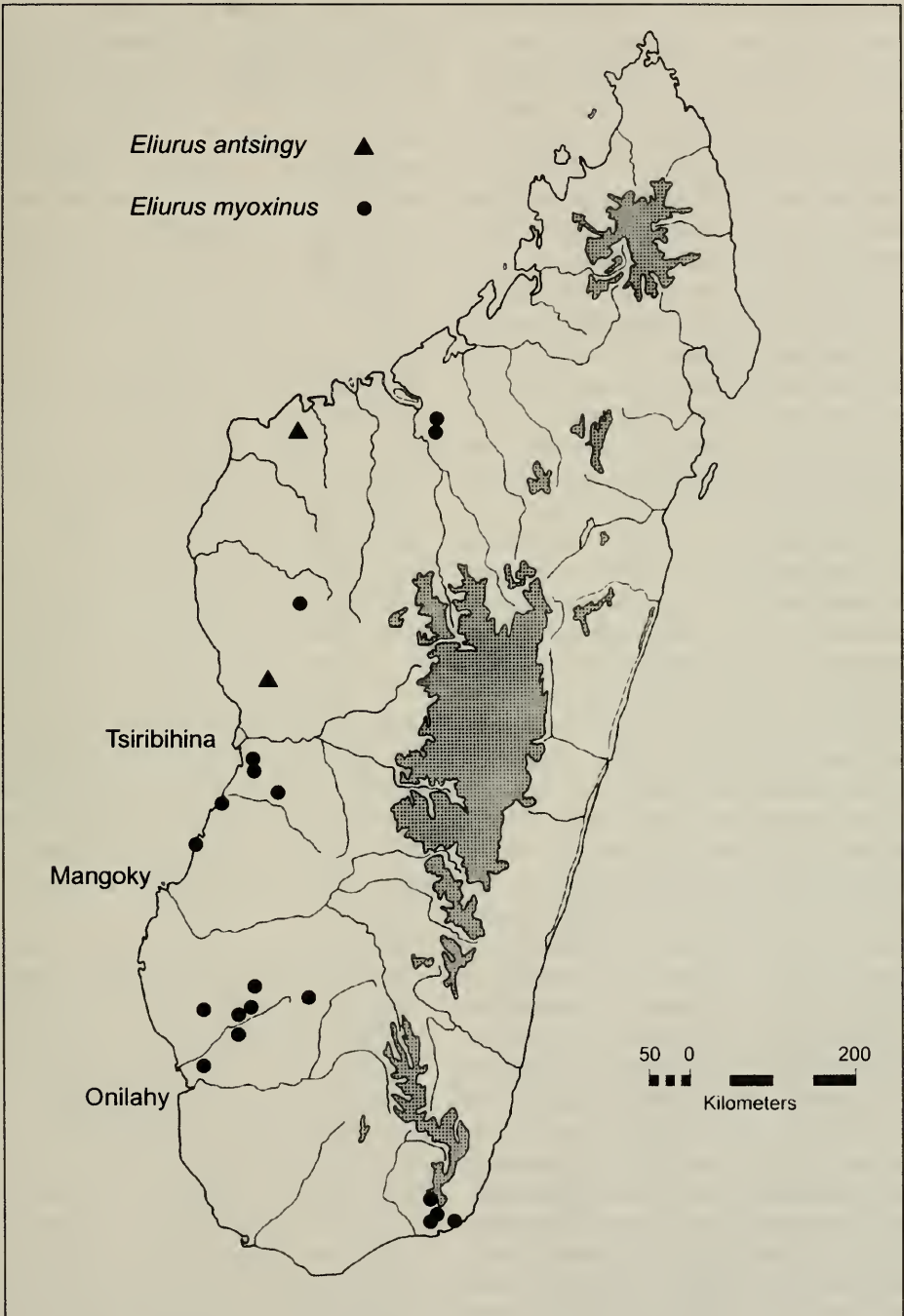


Fig. 3. Geographic occurrence of the species *Eliurus antsingy* and *E. myoxinus*, the two species so far documented as indigenous to western Madagascar. Names refer to the three western rivers discussed in the text, and shaded areas indicate highlands above 1200 m.

the species. Certain habitats above the western coastal piedmont and in inland zones of moderate elevation (e.g., Vohibasia and Analavelona) are floristically transitional between eastern humid forest and western dry deciduous forest (Du Puy et al. 1994, Jenkins & Goodman 1999) and suggest accommodation to more mesic conditions than previously recorded for the species.

A recent mission to the summital zone of the Analavelona Massif (Nov 2000) uncovered a remarkable density of *Eliurus myoxinus*, the single nesomyine rodent living in pristine forest at 1250 m. During five nights of trapping, 500 trap-nights were accrued and only two species of rodents were captured: 91 individuals of *E. myoxinus* and 116 individuals of the introduced *Rattus rattus*. The abundance of this nesomyine species suggests little or no suppression of its population size in the presence of non-native *Rattus*, a finding that contrasts with the diminished catch usually recorded for native rodents in eastern humid forests where *Rattus* is equally plentiful (Goodman 1995). Long-term ecological study is needed to track population fluctuations and determine whether western *Eliurus* are less affected by high densities of *Rattus*.

The habitat in the summital zone of Analavelona is mid-altitude montane sclerophyllous forest as defined by Koechlin et al. (1974). At this elevation in eastern forest, high levels of small mammal diversity have been regularly encountered, with up to six nesomyine species and including as many as three sympatric *Eliurus* (e.g., Goodman & Carleton 1998). The Analavelona Forest exhibits floristic and faunistic affinities to eastern humid forests (Koechlin et al. 1974, Raxworthy & Nussbaum 1997), in particular the Central Domain (sensu Humbert 1955), and appears to represent a mesic relict from a recent geological period when the climate over parts of southwestern Madagascar was distinctly wetter (Burney 1993, Goodman & Rakotozafy 1997). On the basis of the highly successful capture rates of *Eliurus* at the site, 91 of 207 ro-

dent trapped and all referable to *E. myoxinus*, the sympatric occurrence of a congener seems unlikely. In spite of the biogeographic affinities demonstrated between the Analavelona Forest and eastern humid forests for certain organisms, such past links cannot be conjectured based on the rodent community as presently understood. However, evidence for past east-west biotic connections is found in the nearby PN de Isalo, where a form related to eastern *E. majori* has been identified (Jansa & al. 1999).

We here report additional geographic occurrences of *E. myoxinus* that considerably extend its range northwards to the region of the RF de l'Ankarafantsika (16°20.3'S), Mahajanga Province, a distance of about 480 km from the species' previous northernmost locality (Forêt d'Analabe, 19°58'S). Specimens of *E. myoxinus* were first collected in January 1991 (Ampijoroa, 70 m) and later in February 1997 (5 km SSW Ampijoroa, 160 m). The natural wooded habitat in this reserve consists of dry deciduous forest, and the site of the 1997 collections was distinctly degraded due to human activities. Within the reserve and its vicinity, *E. myoxinus* occurs in sympatry with *Macrotarsomys bastardi* and *M. ingens*.

The northern samples of *E. myoxinus* average slightly but consistently smaller in most dimensions of the skull compared with southern populations (Table 3). Still in aspects of cranial shape, the series from Ankarafantsika exhibits the blocky construction characteristic of *E. myoxinus*, such as the parallel-sided zygoma, rectangular braincase, and relatively wide interorbital region. The dorsal pelage, however, is generally more saturated and darker in shade than the sandy brown typical of *E. myoxinus*, though the texture is similarly fine and the length relatively short. The tail tuft is long and bushy, as is characteristic of the species, but the caudal hairs are not quite so long, perhaps a reflection only of its smaller body size. The pelage of one animal (UADBA 9936) in the series is inordinately

Table 3.—Comparison of selected external and craniodental measurements for the holotype (MNHN 1886.1120) and two population samples of *Eliurus myoxinus* (sample statistics include the mean \pm 1 SD and the observed range).

| Variable | MNHN 1886.1120 | Analavelona (n = 12) | Ankarafantsika (n = 8–11) |
|----------|-------------------|---------------------------------|------------------------------|
| HBL | — | 127.7 \pm 6.4 117–136 | 123.6 \pm 8.7 109–130 |
| TL | — | 145.5 \pm 12.8 125.0–167.0 | 132.7 \pm 9.5 115–142 |
| HFL | — | 25.4 \pm 0.8 24.0–26.0 | 23.7 \pm 0.5 23.0–24.0 |
| EL | — | 23.7 \pm 0.8 23.0–25.0 | 20.0 \pm 1.9 18.0–23.0 |
| WT | — | 65.5 \pm 8.3 51–75 | 59.4 \pm 13.3 36–79 |
| ONL | 34.2 | 36.1 \pm 1.2 34.0–37.8 | 34.5 \pm 0.8 33.0–35.3 |
| ZB | 17.6 | 17.8 \pm 0.8 16.7–19.0 | 17.6 \pm 0.4 17.1–18.2 |
| BBC | 13.6 | 14.0 \pm 0.4 13.1–14.5 | 13.7 \pm 0.2 13.5–14.0 |
| IOB | 5.5 | 5.6 \pm 0.1 5.2–5.7 | 5.4 \pm 0.1 5.3–5.6 |
| LR | 11.4 | 12.4 \pm 0.7 10.7–13.3 | 11.4 \pm 0.2 11.2–11.7 |
| BR | 6.6 | 6.7 \pm 0.2 6.3–7.0 | 6.4 \pm 0.3 6.1–7.0 |
| PPL | — | 13.2 \pm 0.7 11.8–14.0 | 12.7 \pm 0.4 12.0–13.1 |
| LBP | 7.1 | 7.6 \pm 0.5 6.7–8.3 | 7.0 \pm 0.3 6.6–7.7 |
| LIF | 5.4 | 5.0 \pm 0.3 4.5–5.7 | 4.9 \pm 0.2 4.6–5.1 |
| BIF | 2.0 | 2.2 \pm 0.1 1.9–2.5 | 2.3 \pm 0.1 2.2–2.4 |
| LD | 10.1 | 10.3 \pm 0.6 9.1–11.0 | 10.0 \pm 0.3 9.5–10.4 |
| BM1s | 6.7 | 7.1 \pm 0.3 6.5–7.5 | 6.6 \pm 0.2 6.4–6.9 |
| DAB | 5.0 | 5.5 \pm 0.3 5.2–5.9 | 5.1 \pm 0.1 5.0–5.3 |
| BZP | 3.1 | 3.3 \pm 0.1 3.0–3.6 | 3.4 \pm 0.2 3.1–3.7 |
| BOC | — | 7.9 \pm 0.3 7.3–8.3 | 7.7 \pm 0.3 7.1–8.1 |
| LM1-3 | 4.90 | 5.19 \pm 0.25 4.74–5.55 | 4.72 \pm 0.10 4.57–4.90 |
| WM1 | 1.27 | 1.41 \pm 0.07 1.30–1.52 | 1.28 \pm 0.07 1.18–1.38 |

“bleached,” its dorsum appearing uniformly tan or light tawny.

Although the Ankarafantsika series is nearer the small end of size variation within the species, multivariate analyses emphasize the basic craniodental conformity of the sample to others of *E. myoxinus* (Fig. 2). The amount of inter-sample differentiation among all OTUs of *E. myoxinus*, including that from Ankarafantsika, resembles the pattern of variation shown by samples of a broadly distributed eastern species, *E. tanala*. Recent molecular work on nesomyine rodents has included samples across the range of *E. myoxinus* (including, from north to south, Ankarafantsika, Kirindy, Isalo, Zombitse, and Andohahela [parcel II]—see Appendix 1), and the amount of sequence divergence and resulting cladogram are consistent with the hypothesis that these various populations represent a single species (Jansa 1998, Jansa & al. 1999).

Two other noteworthy examples of *E. myoxinus* have been recently (Nov-Dec 1999) captured at a second northern locale, the Forêt d'Ankazotshifototra (1150 m) in the RS d'Ambohijanahary. This site (18°15.7'S) lies geographically intermediate to Forêt d'Analabe and the RF de l'Ankarafantsika and suggests that future biological survey will disclose a broad distribution of the species throughout western landscapes. The Forêt d'Ankazotshifototra is situated at the very western edge of the Central Highlands, lying to the north and east of the Bemaraha reserve complex, and consists of humid forest of the Central Domain (sensu Humbert 1955). Faunistically, the Forêt d'Ankazotshifototra is a mixture of eastern and western elements. Within the RS d'Ambohijanahary, *E. myoxinus* was taken sympatrically with two individuals (FMNH 167546, 167555) of an *E. majori*-like form. They are appreciably smaller than typical *E. majori* with stronger contrast of the dorsal-ventral pelage color. While further study is required to properly assess the status and relationship of this form, its trenchant features recall species

(*E. majori* and *E. penicillatus*) that were previously known only from eastern Madagascar.

Discussion

The unique combination of morphological features exhibited by *E. antsingy* provides insufficient basis for meaningful comment on the new species' closest relatives. We do suspect that, although presumably western in its distributional setting like *E. myoxinus*, *E. antsingy* is not specially related to this more widely known western form. Firmer understanding of their level of relationship within the radiation of *Eliurus* must await the acquisition of additional specimens, recourse to other sources of taxonomic information, and broader intrageneric comparisons. Other geographic parallels are known within Madagascar's small mammal fauna. For example, molecular evidence suggests that the species of mouse lemur known from the Bemaraha area, *Microcebus myoxinus*, is one of the sister taxa to the eastern *M. rufus* group rather than the widespread *M. murinus* group (Yoder et al. 2000).

As currently understood, the taxonomic diversity of Madagascar's indigenous rodents is concentrated along the eastern one-third of the island as compared to its spacious western landscapes (Table 4). Seven genera representing seventeen species have been documented to date in the east versus four genera representing eight species in the west. Such a contrast in species richness could be plausibly attributed to the circumstantial interplay of the island's physical geology and regional climatic patterns, and attendant opportunities for the stratification of plant communities, greater ecological complexity, and geographic isolation that follow.

However, while recent biological inventories have substantially bolstered our knowledge of nesomyine distributions in eastern Madagascar (Goodman & Carleton 1996, 1998, Goodman et al. 1996, 1999,

Table 4.—Tabulation of nesomyine species known from eastern versus western landscapes of Madagascar.

| Eastern | Western |
|-----------------------------------|-------------------------------|
| <i>Brachytarsomys albicauda</i> | <i>Eliurus antsingy</i> * |
| <i>B. villosa</i> ** | <i>E. aff. majori</i> |
| <i>Brachyuromys betsileoensis</i> | <i>E. myoxinus</i> |
| <i>B. ramirohitra</i> | <i>E. aff. tanala</i> |
| <i>Eliurus ellermani</i> * | <i>Hypogeomys antimena</i> |
| <i>E. grandidieri</i> * | <i>Macrotarsomys bastardi</i> |
| <i>E. majori</i> ** | <i>M. ingens</i> |
| <i>E. minor</i> | <i>Nesomys lambertoni</i> ** |
| <i>E. penicillatus</i> ** | |
| <i>E. petteri</i> * | |
| <i>E. tanala</i> ** | |
| <i>E. webbi</i> ** | |
| <i>Gymnuromys roberti</i> | |
| <i>Monticolomys* koopmani</i> * | |
| <i>Nesomys audeberti</i> ** | |
| <i>N. rufus</i> | |
| <i>Voalavo* gymnocaudus</i> * | |

* = Described as new since 1994.
 ** = Resurrected from junior synonymy since 1994.

Carleton & Goodman 2000), vouchered documentation of nesomyine occurrences in the west has only started to fill in the significant geographic gaps identified by Carleton & Schmidt (1990). Until now, *Eliurus myoxinus*, described by Milne Edwards in 1885, has remained the only species of that genus recorded from western environments; over just the past six years, three eastern species of *Eliurus* have been newly described and another four recently resurrected from junior synonymy as valid (Carleton 1994, Carleton & Goodman 1998). The diagnosis of *E. antsingy*, reported herein, and the presence of autochthonous genera like *Hypogeomys* and *Macrotarsomys*, together suggest the rich potential for future discoveries among the island's western habitats. The recovery of additional species from Ambohijanahary and Bekopaka that appear to have affinity to forms of eastern *Eliurus*, like the recent report of an *E. majori*-like form from Isalo (Jansa & al. 1999), further attest our imperfect knowledge of nesomyine distributions in western Madagascar. In view of the many regions that still lack thorough site

survey, any meaningful conclusion on the degree of east-west biodiversity contrasts must await this firmer foundation of field inventory and systematic study.

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Appendix 1

Listed below are specimens of *Eliurus* that formed the basis for the morphological comparisons, sample statistics, morphometric analyses, and mapped distributions presented above.

Eliurus myoxinus.—Fianarantsoa Province: Parc National de Isalo, 3.8 km NW Ranohira, along Namaza River, 800 m; 22°32.4'S, 45°22.8'E (FMNH 166079–166081). Mahajanga Province: Forest Station, Ampijoroa, 70 m, 16°15'S, 46°48'E (DR 165; USNM 576754–576756); Réserve Forestière de l'Ankarafantsika, 5 km SSW Ampijoroa, 160 m, 16°20.3'S, 46°47.6'E (UADBA 9935–9943); Réserve Spéciale d'Ambohijanahary, Forêt d'Ankazotsihafototra, 1150 m; 18°15.7'S, 45°25.2'E (FMNH 167545, 167547). Toiliara Province: Forêt d'Analabe, 60 km N Morondava (MNHN 1980.290, 1982.988); Forêt d'Analavelona, 12 km NW Andranoheza, 1050 m, 22°40.7'S, 44°11.5'E (FMNH 161578–161589); Réserve Naturelle Intégrale d'Andohahela, parcel II, 7.5 km ENE Hazofotsy, 120 m, 24°49.0'S, 46°36.6'E (FMNH 156630); Beroboka, 40 mi N Morondava (BMNH 47.1608, 47.1609, 1987.50); 5 mi E Bevilany, Ambovombe-Fort Dauphin road, the hills, 800 ft (BMNH 47.1600–47.1607, 66.2746); Kirindy Forest, 60 km NE Morondava, 20°04'S, 44°49'E (FMNH 154632, 154633); Lamboromakandro, Forêt de Sakaraha (MNHN 1961.220); Morondava (MNHN 1973.516); Petriky Forest, 5–7 km SE Manambara, 20 m, 25°04'S, 46°53'E (USNM 578679–578687); Tsilambana (MNHN 1886.1120, holotype); 35 mi E Tulear (BMNH 47.1610, 47.1611, 47.1611a); Forêt de Vohibasia, 59 km NE Sakaraha, 780 m, 22°27.5'S, 44°50.5'E (FMNH 156183, 156191); Forêt de Vohimena, 35 km SE Sakaraha (FMNH 156192–156194); Forêt de Zombitsy, 870 m, 22°51'S, 44°43'E (FMNH 151951, 151952).

Eliurus tanala.—Antsiranana Province: Réserve

Spéciale d'Anjanaharibe-Sud, 6.5 km SSW Befingitra, 875 m, 14°45.3'S, 49°30.3'E (FMNH 154049); Réserve Spéciale d'Anjanaharibe-Sud, 9.2 km WSW Befingitra, 1260 m, 14°44.7'S, 49°27.7'E (FMNH 154050, 154051, 154249, 154250; UA-SMG 6979). Fianarantsoa Province: Ambodiamontana, 7 km W of Ranomafana, 950 m, 21°16'S, 47°26'E (USNM 448981–448990, 448997, 449250); 3 km NNW Vohiparara, 1225 m, 21°13'S, 47°22'E (USNM 449251–449255); 1 km NW Andrambovato, 875 m, 21°30'S, 47°25'E (USNM 449256); Réserve Naturelle Intégrale d'Andringitra, 38 km S Ambalavao, ridge east of Volotsangana River, 1625 m, 22°11'S, 46°58'E (FMNH

151691, 151692, 151744, 151880, 151881); Réserve Naturelle Intégrale d'Andringitra, 40 km S Ambalavao, along Volotsangana River, 1210 m, 22°13'S, 46°58'E (FMNH 151690, 151743, 151873, 151874, 151897); Réserve Naturelle Intégrale d'Andringitra, 43 km S Ambalavao, junction of Sahanivoraky and Sahavato rivers, 810 m, 22°13'S, 47°00'E (FMNH 151687, 151688, 151869, 151870). Toamasina Province: 10 mi NW Lohariandava, 1500 ft (BMNH 47.1573); Périnet, near Moramanga, 3000 ft (BMNH 47.1557, 47.1560–47.1562, 47.1564–47.1568, 47.1571, 47.1572; MNHN 1961.176); 1 km E Périnet (USNM 341826); 2 km E Périnet (USNM 328828, 328829); 13 km E Périnet (USNM 341827).